

Revision of Dorid Nudibranchia Collected during the French Cape Horn Expedition in 1882–1883, with Discussion of the Genus *Geitodoris* Bergh, 1891

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Abstract. Historical material of cryptobranch Doridoidea collected from south of Tierra del Fuego during the “Mission Scientifique du Cap Horn 1882–1883” and originally assigned to *Doris hispida* d’Orbigny, 1837, *Doris plumulata* Couthouy in Gould, 1852, and *Doris luteola* Couthouy in Gould, 1852, has been examined anatomically. One specimen is identified as the common Magellanic species *Diaulula hispida* (d’Orbigny, 1837). Two specimens belong to the poorly known *Geitodoris patagonica* Odhner, 1926. This latter species is redescribed for the first time using additional material recently collected. Re-examination of type material of *G. patagonica* and of *Geitodoris falklandica* Odhner, 1926, confirms the common possession of enlarged prostate glands and of large, saclike mantle glands. Both species are regarded to be conspecific, with *Geitodoris patagonica* Odhner, 1926, as the valid name. A lectotype of *G. patagonica* has been designated. This species is compared with congeners; *Discodoris mavis* Marcus & Marcus, 1967, and *Discodoris tema* Edmunds, 1968, are transferred to *Geitodoris* Bergh, 1891, due to the possession of spatulate marginal radular teeth which is considered to be an autapomorphy of the genus. This record from Nassau Bay and the synonymization with *G. falklandica* extends the known range of *G. patagonica* from Argentina to southernmost Chile and the Falkland Islands. The enigmatic species *Doris plumulata* and *Doris luteola* are discussed and regarded as *nomina dubia*.

INTRODUCTION

During the “Mission Scientifique du Cap Horn 1882–1883” several nudibranchs were collected from Nassau Bay, south of Tierra del Fuego, Chile, and tentatively identified by Rochebrune & Mabile (1891). All but *Microlophus poirieri* Mabile & Rochebrune, 1891 (Dendronotoidea) and *Phidiana patagonica* (d’Orbigny, 1837) (Aeolidoidea) were doridoideans. The phanerobranch dorid *Acanthodoris vatheleti* Mabile & Rochebrune, 1891, was only briefly described externally by Rochebrune & Mabile (1891). Pruvot-Fol (1950) described additional phanerobranch specimens collected during the Cape Horn Expedition which had not been mentioned by Rochebrune & Mabile (1891) as *Thecacera darwini* Pruvot-Fol, 1950. This species was redescribed in detail by Marcus (1959), and, in living condition, by Schrödl (1996b).

Most problematic are the cryptobranch dorids from the Cape Horn Expedition which Rochebrune & Mabile (1891) identified as *Doris hispida* d’Orbigny, 1837, *Doris plumulata* Couthouy in Gould, 1852, and *Doris luteola* Couthouy in Gould, 1852 without giving any description. *Diaulula hispida* (d’Orbigny, 1837) is a better known species which is recognizable externally by a median dorsal ridge (d’Orbigny, 1835–1846; Odhner, 1926; Marcus, 1959; Schrödl, 1996b). In contrast, both *D. plumulata* and *D. luteola* are highly dubious species. Due to Gould’s

(1852, 1856) poor original descriptions, their correct identification appears extremely unlikely.

This study aims to clarify the taxonomy of cryptobranch dorids collected during the Cape Horn Expedition on the basis of museum material. From dissections of historical specimens, detailed anatomical descriptions are presented for *Diaulula hispida* and *Geitodoris patagonica*; for the latter species, type material and recently collected specimens were also examined. *Geitodoris patagonica* is revised taxonomically and compared with congeners.

SPECIES DESCRIPTIONS

Family DISCODORIDIDAE Bergh, 1891

Genus *Diaulula* Bergh, 1880

Type species: *Diaulula sandiegensis* (Cooper, 1863)

Diaulula hispida (d’Orbigny, 1837)
(Figures 1–3)

Doris hispida d’Orbigny, 1837:188, pl. 15, figs. 4–6; Rochebrune & Mabile 1891:10.

Trippa hispida (d’Orbigny, 1837): Bergh 1898:527–530, pl. 30, figs. 30–36, pl. 31, figs. 1–3; Odhner 1926:76–78, figs. 55–58, pl. 3, figs. 40–41 (“d’Orbigny, 1836”); Carcelles 1950:70; Carcelles & Williamson 1951:315 (“d’Orbigny, 1847”).

Diaulula hispida (d’Orbigny, 1837): Marcus 1959:50–53,

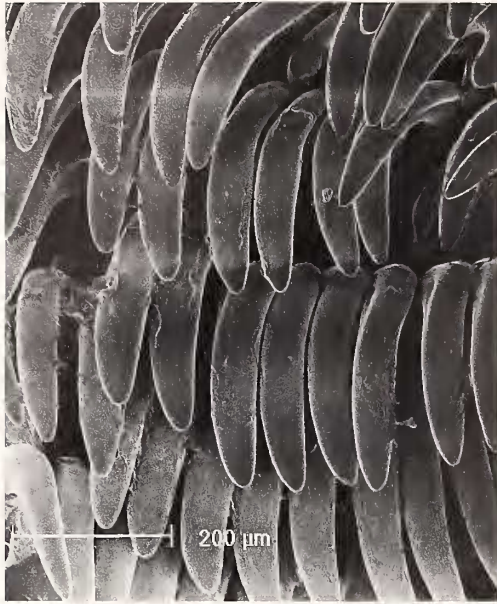


Figure 1

SEM photograph (unsputtered) of radular teeth of *Diaulula hispida* ("Doris sp.", MNHN). Scale bar = 200 μ m.

figs. 109–114; Schrödl 1996a:52–53; 1996b:27, pl. 3, fig. 18; 1997a:39.

Material examined: One specimen from the National Museum of Natural History (MNHN) of Paris labeled: *Doris sp.*, Baie d'Orange, Baie de Nassau, Chili. Mission du Cap Horn (entrée 1883).

External morphology: The single museum specimen is yellow, the foot darker than the notum. It is well extended and measures 23 mm in length, 12 mm in breadth, and 10 mm in height. The foot is broad, measuring 10 mm. However, this specimen is very poorly preserved. The mantle rim is seriously damaged so it might have been broader, and the anterior body is artificially swollen. Most parts of the notum are devoid of any recognizable tubercles, superficial tissue is almost completely destroyed. In a protected area lateral to the gills there are remains of small conical tubercles with diameters between 0.1 to 0.3 mm. There are about six multipinnate gills surrounded by an elevated sheath. The rhinophores are too damaged to give information on the number of perfoliations or the presence of a sheath. The foot is bilabiate anteriorly, but damaged near the mouth opening; the superior lip appears to be notched. The anterior mantle rim and the anterior part of the head is lacking, but there appears to be one digitiform oral tentacle left.

Anatomy: Because the external features of this cryptobranch dorid do not allow identification, dissection was necessary. Owing to its very frail and amorphous consistency, my main attempt was to get information on cutic-

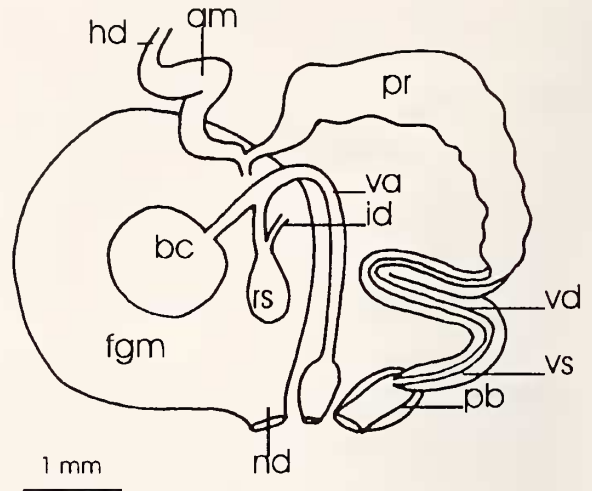


Figure 2

Reconstructed reproductive system of *Diaulula hispida* ("Doris sp.", MNHN). Scale bar = 1 mm. Key: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; hd, hermaphroditic duct; id, insemination duct; nd, nidamental duct; pb, penial bulb; pr, penial papilla; pr, prostate; rs, receptaculum seminis; va, vagina; vd, vas deferens; vs, vas deferens sheath.

ularized structures like lip cuticle, radula, and possible genital armature.

The oral tube and pharynx are squeezed downward by an overlying swollen granular mass containing glandular particles, probably remains of the blood gland and salivary glands. Sand granules indicate the presence of the completely amorphous esophagus. Remains of the central nervous system could not be detected.

Digestive system. The strong lip cuticle is brownish and smooth. The buccal mass is dark brown and hardened. It is dorsoventrally flattened, 6 mm in length, and 5 mm in breadth. The radula (Figure 1) measures 5.3×5.0 mm. It consists of 24 rows with up to 27 teeth per half row. The rhachis is small and lacks a central tooth. All lateral teeth are brownish, simple hamate without denticulation, and rather erect in shape with a blunt tip. The inner laterals are small, increasing in size toward the middle of the half rows (up to 0.3 mm). The outermost laterals are small.

Reproductive system (Figure 2). Parts of the small conical penial papilla and the penial bulb were everted through the genital opening. The penis was dissolved in 10% KOH and did not possess cuticular armature. Internally, the anterior genitalia are conglomerated and strongly hardened due to preservation. They are limited to the right side of the body. The ampulla is a curved tube attached to the large female gland mass. This organ appears to be composed of a dark, widely lobed mucus gland and a whitish, more granular albumen gland. There appears



Figure 3

Geographic distribution of *Diaulula hispida*.

to be a large irregularly shaped prostate passing into an artificially squeezed, looped vas deferens section. The vas deferens consists of a narrow central duct which is surrounded by a thick muscular sheath. Distally the central duct passes into the small penial papilla; the muscular sheath fuses with the vestibular wall. There is a long, narrow vagina which widens distally into a vestibule separate from the male opening. A bursa copulatrix and a receptaculum seminis were present but completely flattened. Their poor condition allowed a reconstruction of their vaginal arrangement, but not, with any certainty, their shape. Vagina and distal vas deferens were treated with KOH; both lack any cuticle.

Discussion: The specimen examined within the present study was damaged and in very poor preserved condition. Internally, it fits with the description of *Diaulula hispida* (d'Orbigny, 1837), a species which was redescribed in detail by Marcus (1959) and recently, in living condition, by Schrödl (1996b). In particular, radular features like the number of rows, teeth per half row, and erect, simple hamate shape, and smooth lip cuticle; and also genital characters like the special arrangement of seminal receptacles, separate vestibules, and vas deferens proximally forming a prostate and distally a narrow duct which is surrounded by a thick muscular sheath agree perfectly with Marcus' redescription. The general body shape and coloration, a relatively broad, bilabiate, and notched foot, the dense, small notal tubercles, and the elevated gill sheath confirm the identification as *D. hispida*. The presence of an undulating dorsal crest, the most distinctive external character of *D. hispida*, however, could be neither confirmed nor denied; the museum specimen was in too poor condition, especially the central parts of the notum. The only known congener from Chilean and Argentinian waters, *Diaulula vestita* (Abraham, 1877) clearly differs in lacking a notal crest (see Odhner, 1926; Marcus, 1959); the latter species should be critically compared with *Anisodoris punctuolata* (d'Orbigny, 1837).

Diaulula hispida was recently found in the Magellan Strait south of Punta Arenas (Schrödl, 1996a, b) near the collecting locality of the museum specimen, and has a wide Magellanic distribution (Schrödl, 1996b, 1997a; this study, see Figure 3). The record from Tumbes, Peru, by Carcelles (1950) and Carcelles & Williamson (1951) is not based on original data and was regarded as an error (Schrödl, 1996b).

Rochebrune & Mabile (1891) mentioned the cryptobranch species *Diaulula hispida* (as *Doris hispida*) as being found during the Cape Horn Expedition. It is, however, not clear if this identification really referred to this specimen, which is now too damaged to show the characteristic notal crest, or if this specimen formerly was assigned to *Doris plumulata* or *Doris luteola*, the other two cryptobranch species mentioned by Rochebrune & Mabile (1891). There is neither information within that

publication nor on the museum's labels indicating which specimen each of the names applies to. This makes no difference in the case of *D. hispida* since this species is clearly identified in the present study. It will always remain problematic regarding the specimens assigned to *Doris plumulata* and *Doris luteola*. Both species originally were described only externally and in a sketchy way on board ship by Couthouy and were subsequently established in the publications of Gould (1852, text; 1856, drawings). Millen et al. (1994) considered external descriptions of central Chilean species by Gould to be inadequate for re-identification. This is also true for the southern species *Doris plumulata* and *Doris luteola*: *D. plumulata* comes closest to *Anisodoris punctuolata* (d'Orbigny, 1837) due to its fine notal tuberculation and eight delicate tripinnate gills. Having nine pairs of lanceolate, simply pinnate plumules *Doris luteola* more resembles *Gargamella immaculata* Bergh, 1894, which possesses eight to 12 bi- or tripinnate gills (Schrödl, 1996b, 1997b). However, there are some other Magellanic cryptobranch species with small notal tubercles and digitiform oral tentacles, i.e., two *Geitodoris* species described by Odhner (1926), which would also fit the superficial external descriptions of both of these species; there is no information on diagnostic internal organs, i.e., radula and genitalia. Since according to Johnson (1964; personal communication) no type material has been ever designated for *Doris plumulata* (misspelled "*Doris planulata*" by Carcelles (1950) and "*Doris plumulata*" by Carcelles & Williamson, (1951) and *Doris luteola* (misspelled "*Doris lucteola*" by Carcelles (1950) and Carcelles & Williamson, (1951), both species cannot be re-identified and are considered to be *nomina dubia*.

Family DISCODORIDIDAE Bergh, 1891

Genus *Geitodoris* Bergh, 1891

Type species: *Geitodoris complanata* (Verrill, 1880)

Geitodoris patagonica Odhner, 1926 (Figures 4–9)

Geitodoris patagonica Odhner, 1926:80–83, figs. 59–63, pl.3, figs. 42–43; Carcelles 1950:70; Carcelles & Williamson 1951:315; Schrödl 1996b:57, pl.3, fig. 17.

Geitodoris falklandica Odhner, 1926:83–85, figs. 64–69, pl. 3, figs. 44–46.

Material examined (see Table 1): Two specimens from the Muséum National d'Histoire Naturelle, Paris (MNHN) labeled: *Doris* sp., Baie d'Orange, Baie de Nassau, Chili. Mission du Cap Horn (entrée 1883). The larger dissected specimen has been re-examined; the smaller specimen has been dissected and is described anatomically.

Eight specimens of *Geitodoris patagonica* Odhner,

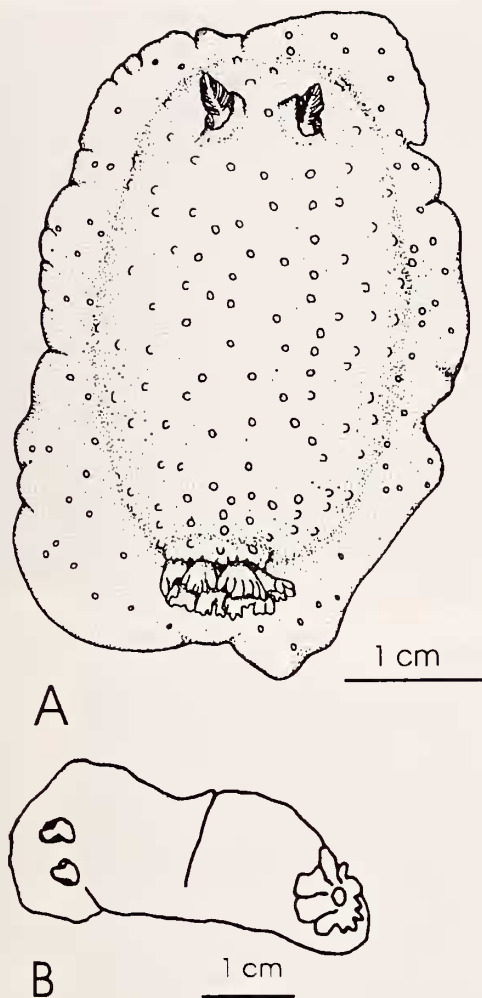


Figure 4

Drawings of *Geitodoris patagonica*. A. Living recently collected specimen No. 2. B. Damaged smaller museum specimen "*Doris* sp.", NMNH. Scale bars = 1 cm.

1926, from Bahía Camarones, Argentina, collected by S. Gigglinger and M. Schrödl, 9 January 1995, at 2 to 12 m depth, most on macroalgae, using SCUBA. A photograph of a living specimen was given by Schrödl (1996b). Two specimens have been examined anatomically and deposited as voucher specimens in the Zoologische Staatssammlung München (ZSM) under the numbers 19971031 and 19971032.

Geitodoris falklandica, holotype from the Swedish Museum of Natural History, Stockholm (SMNH, type collection 2304), collected at Stanley Harbour, Falkland Islands.

Geitodoris patagonica, lectotype, SMNH type collection 2306, collected at Puerto Madryn, Argentina, 23 January 1896. *Geitodoris patagonica*, four specimens, three

of them partly dissected, SMNH type collection 1016, collected at Puerto Madryn, Argentina, 9 January 1895.

External morphology (Figure 4): The larger specimen from the MNHN ("*Doris* sp.") is whitish and measures about 60 mm in length, 30 mm in width, and 15 mm in height. Beside being seriously damaged and hardened due to preservation, the anterior part of the body had been partly dissected by a former worker. The notum is covered with different-sized tubercles, the largest reaching a diameter of 1 mm. The tubercles are slightly elevated, rounded knobs. Spicules are absent, most probably due to preservation. The notum is squeezed and compact in the central parts. Laterally it has a more spongy consistency with several sac- or bottle-like, hollow structures within (see Figure 5). These reach about 0.5 mm in diameter and probably are large subepidermal glands. Some clearly open onto the notal surface, and it appears that these openings are not preservation artifacts. There are seven mainly bipinnate gills around the elevated anal papilla. Gills and rhinophores are surrounded by considerably elevated sheaths covered with small tubercles. The foot is broad and anteriorly bilabiate. The upper lip is notched. Oral tentacles are long and digitiform.

The smaller MNHN specimen ("*Doris* sp.") measures 37 mm in length, 19 mm in width and about 10 mm in height. It is moderately extended, but in rather bad external condition (Figure 4B). Where undamaged, the notum is covered with different-sized tubercles. The largest ones reach a diameter of 1 mm and are surrounded by smaller tubercles with usually 0.1 to 0.3 mm diameter. All are knobby and most are only slightly elevated. Spicules are absent, but cavities within the tubercles and the notum indicate that spicules were present in the living specimen. Large, saclike subepidermal glands as described above are present throughout the notum (Figure 5C). Far posteriorly there is an unnaturally expanded, prominent anal papilla surrounded by seven or eight mainly bipinnate gills. The most posterior part of the gills and the notum is damaged and turned to the ventral side. The gills, as well as the rhinophores, are surrounded by elevated sheaths which bear different-sized tubercles resembling those of the notum. The perfoliate rhinophores possess about 17 lamellae. The foot is nearly as broad as the notum. Anteriorly it may be bilabiate, but this portion is damaged. No information can be given on the presence of a notch or on the shape of oral tentacles.

As in the larger specimen, genital openings are within the anterior third of the body on the right side. The tip of the penial papilla and parts of an everted penial sheath are visible.

Anatomy: The anterior portion of the larger specimen from the MNHN was dissected by a former worker. The radula was removed from the specimen but not retained in the museum lot. The anterior genitals are still mainly *in situ*, but strongly hardened due to preservation and

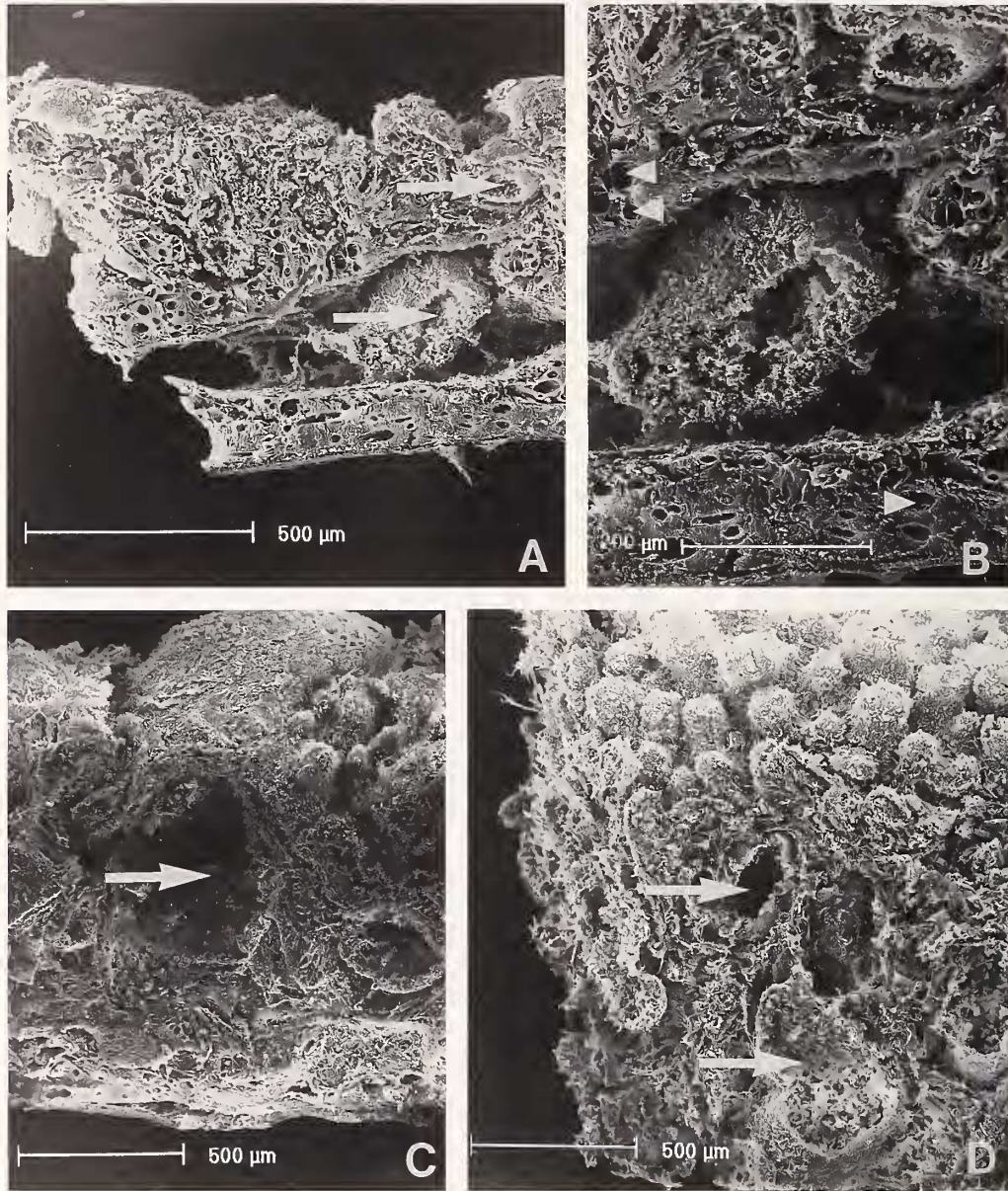


Figure 5

SEM photographs of critical point dried notum structures of *Geitodoris patagonica*. Note the saclike, large subepidermal glands (arrows). A. Holotype *G. falklandica*, overview of a notum section. Scale bar = 0.5 mm. B. Holotype *G. falklandica*, notum section in detail; see also spaces of dissolved spicules (arrow-heads). Scale bar = 0.2 mm. C. *Doris* sp. smaller specimen, MNHN. Scale bar = 0.5 mm. D. Lectotype of *G. patagonica*. Scale bar = 0.5 mm.

hardly suitable for a detailed examination. However, the anatomy of the larger specimen appears to generally agree with that of the smaller specimen which is described in the following section:

Digestive System. The oral tube is wide and flattened, the pharynx is artificially squeezed backward. The yellowish to brownish lip cuticle is covered by small simple rodlets. The radula of the smaller specimen comprises 25

rows. The rachis lacks a rachidian tooth and is very narrow with innermost lateral teeth of apparently alternating rows being close together. There are up to 24 lateral teeth lacking any denticulation, but their shape strongly varies and additionally depends on the angle of view. By light microscopy, the first and second laterals are small, having a stout hook. The following laterals increase in size becoming more erect. The outer laterals decrease, the out-

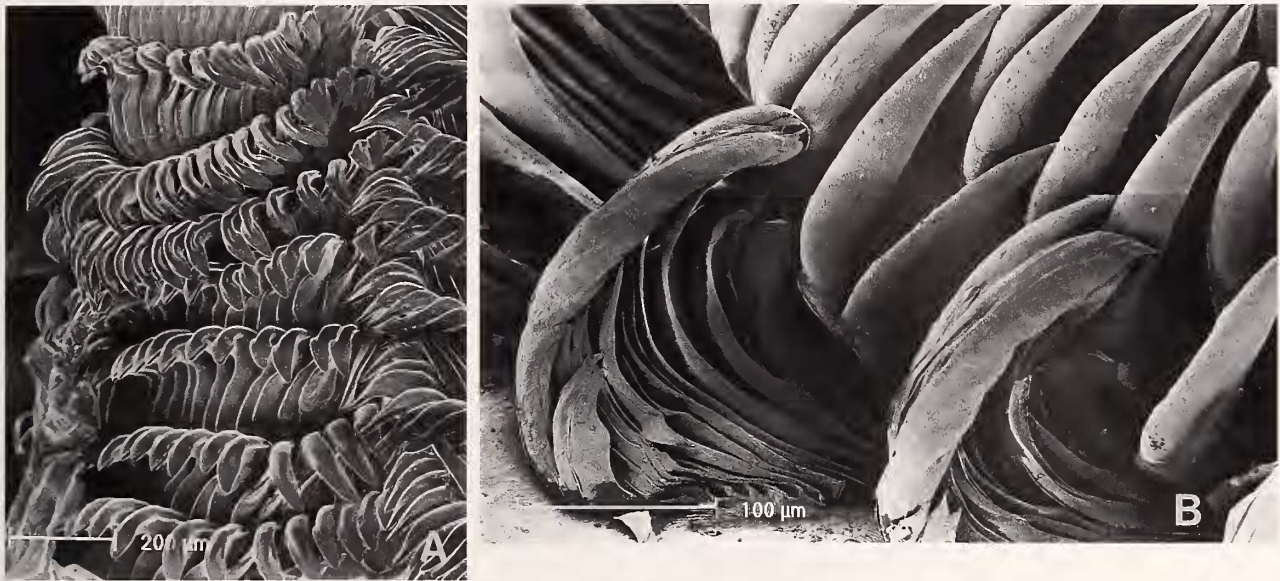


Figure 6

SEM photographs of radular structures of *Geitodoris patagonica*. A. Smaller MNHN specimen, older lateral teeth (unspattered). Scale bar = 0.2 mm. B. Recently collected specimen No. 1, lamellate marginal and hamate outer lateral teeth. Scale bar = 0.1 mm.

ermost becoming spoonlike in appearance. In older rows only rudiments of marginal teeth were detected. In younger rows there are up to about 15 marginal teeth, which are delicate, very close standing lamellae. Some are

slightly fringed, which may be an artifact. By SEM examination, the shafts of most laterals in older rows prove to be laterally flattened. Inner laterals have an arrow-headlike tip (Figure 6A). In younger rows, lateral teeth are more slender and hook-shaped. Lateral and marginal teeth resembling those of younger rows of the museum specimen were present in recently collected *G. patagonica* specimens (Figure 6B).

In the smaller MNHN specimen the esophagus is a round tube which is looped twice before passing through the circumesophageal nerve ring. The salivary glands are long thin tubes. The esophagus curves ventrally, penetrating the digestive gland. The stomach is completely covered by the digestive gland; only a bulbous caecum reaches its dorsal surface posterior to the intestine. Adjacent to the surface of the digestive gland the intestine runs to its anterior edge and curves back to the anal papilla.

Genital System (see Figures 7, 8). The gonads cover the digestive gland. A thin hermaphroditic duct widens into a flattened, curved, white ampulla. Before entering the female gland mass, the prostate arises, apparently directly from the ampulla. The prostate continuously widens into a huge, massive U-shaped organ which is closely attached to an ample bursa copulatrix. The proximal portion of the prostate is yellowish and homogenous, but more distally it is yellow and appears granular. Distally the prostate narrows abruptly giving rise to the narrow, long, and highly convoluted muscular vas deferens. This duct passes into an unarmed conical penial papilla sur-

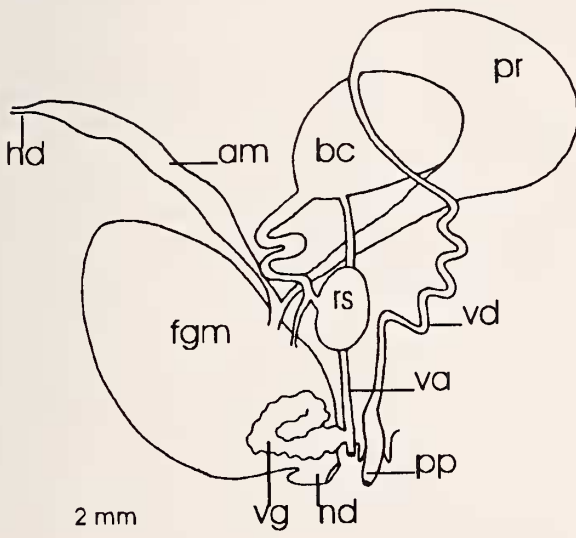


Figure 7

Reproductive system of *Geitodoris patagonica* ("Doris sp.", smaller specimen, MNHN). Scale bar = 2 mm. Key: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; nd, nidamental duct; pp, penial papilla; pr, prostate; rs, receptaculum seminis; va, vagina; vg, vaginal gland; vd, vas deferens.

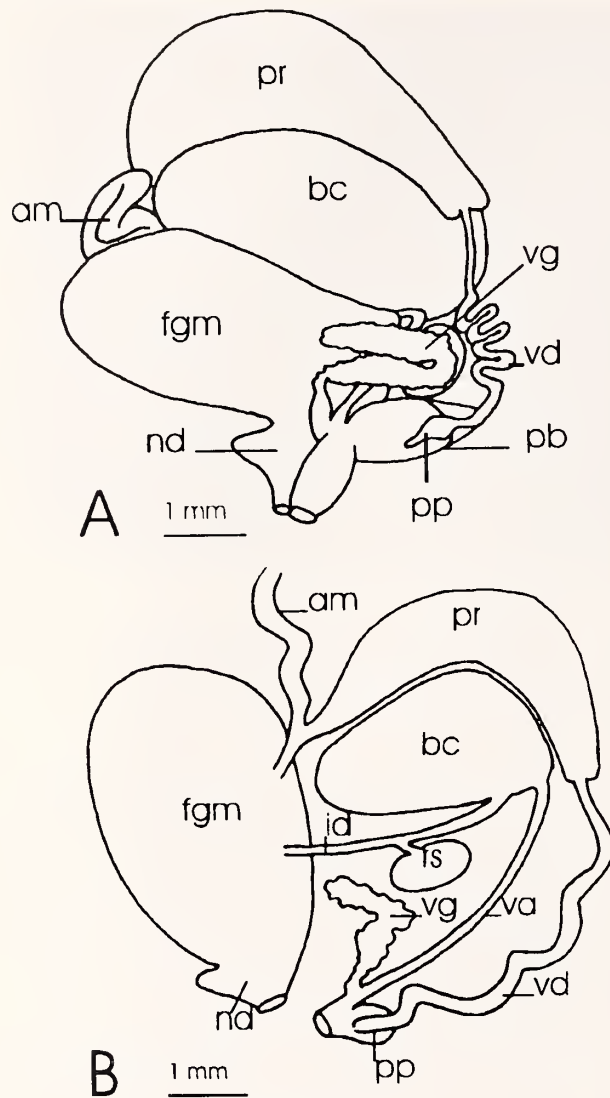


Figure 8

Reproductive system of recently collected *Geitodoris patagonica* No. 1. A. *In situ*. B. Schematical outline. Scale bars = 1 mm. Key: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; id, insemination duct; nd, nidamental duct; pb, penial bulb; pp, penial papilla; pr, prostate; rs, receptaculum seminis; va, vagina; vg, vaginal gland; vd, vas deferens.

rounded by a swollen penial sheath. The vagina opens into a common vestibule close to the male opening. Very near to its opening the vagina bears an unarmed tubular, flattened, and convoluted gland. The vagina is long and leads directly to the bursa copulatrix. This is an oval organ with a maximum dimension of 10 mm and is filled with a yellowish compact mass. The bursa is serially inserted by the convoluted vaginal duct. Far distally, before entering the female gland mass, this duct gives rise to the short stalk of the receptaculum seminis. This somewhat

oval to pear-shaped organ reaches 2 mm in dimension. The female gland is a compact, strongly hardened organ which obviously consists of a widely lobed mucus gland partly surrounded by other, more granular appearing portions. The nidamental duct is short, has a swollen bulb, and opens separately.

Further Organ Systems. The blood gland consists of two lobes, a posterior one covering the posterior portions of the central nervous system, and an anterior one. The cerebropleural ganglia are completely fused. The eyes appear to be sessile.

Taxonomic discussion of *Geitodoris patagonica*: As pointed out above, it is not clear to which species Rochebrune & Mabille (1891) originally assigned the two museum specimens examined. In the present study, both specimens are regarded to be conspecific, although only the smaller specimen could be examined in detail. The lip cuticle having rodlets, the radula with simple hamate lateral and lamellate (= spatulate) marginal teeth, and the genital system having an unarmed penial papilla and a vaginal accessory gland indicate placement in the genus *Geitodoris* as reviewed by Miller (1996). The smaller museum specimen in nearly all external and anatomical features agrees with the description of *Geitodoris patagonica* Odhner, 1926. It differs from the original description of *G. falklandica* Odhner, 1926, the second species of the genus known from Magellanic waters, due to the presence of large subepidermal glands. Both of these Magellanic species, however, are described as completely lacking a prostate (Odhner, 1926). In contrast, a large massive prostate is undoubtedly present in the MNHN material examined.

To clarify this discrepancy, eight specimens considered to be *G. patagonica* and briefly described in living condition (Schrödl, 1996b) have been re-examined, two of them internally (Figure 4A). These specimens, collected from the Patagonian coast of Argentina, externally and anatomically agree with the MNHN specimens, except for some obvious preservation artifacts like body damage and distortions and the dissolution of calcareous spicules. The somewhat larger and more elevated tubercles in the MNHN specimens may be due to their larger size (see Table 1); the shape of lateral radular teeth is not as variable as seen in the smaller MNHN specimen. The genital systems of all specimens examined fit the sketchy drawings of *G. falklandica* (Odhner, 1926:figs. 68, 69) with only one difference: at the position drawn, the vas deferens passes into the prostate, which is closely attached to the female glands and hard to distinguish from the female gland mass (Figure 8A). The prostate is very large and extends around the bursa copulatrix (Figures 7, 8).

A similar, large prostate has also been found on re-examination of the partly dissected holotype of *G. falklandica*. The type material of *G. patagonica* is composed of five smaller specimens, the larger ones extensively dis-

Table 1
Comparison of *Geitodoris patagonica* specimens known anatomically

| Specimen | Collecting location | Preserved body size; | | | Tubercle diameter (mm) | Mantle glands | Radula formula | Prostate |
|--|---------------------------------------|------------------------------------|-----------|-------------------------------|---|-----------------------|----------------|----------|
| | | l length, b breadth, h height (mm) | | | | | | |
| <i>Doris</i> sp., MNHN, No. 1 | Baie d'Orange, Magellan Strait, Chile | l 60, b 30, h 15 | 0.2-1 | present | radula removed and apparently disappeared | present | | |
| <i>Doris</i> sp., MNHN, No. 2 | Baie d'Orange, Magellan Strait, Chile | l 37, b 19, h 10 | 0.2-1 | present | 25 × 10-15.24.0.24.10-15 | present | | |
| <i>G. patagonica</i> det. Schrödl, 1996, No. 1, ZSM 19971031 | Bahía Camarones, Argentina | l 26, b 12, h 9 | 0.1-0.5 | present | 15 × 11-17.26.0.26.11-17 | present | | |
| <i>G. patagonica</i> det. Schrödl, 1996, No. 2, ZSM 19971032 | Bahía Camarones, Argentina | l 28, b 20, h 14 | 0.15-0.6 | present | 16 × 10-15.28.0.10-15 | present | | |
| <i>G. patagonica</i> , lectotype, SMNH No. 2306 | Pto. Madryn | l 10, b 7, h 6 | up to 0.2 | present | 16 or 23 × ca. 20.20.0.20.20 (Odhner, 1926) | present | | |
| <i>G. patagonica</i> , SMNH No. 1016, largest specimen | Pto. Madryn | l 12, b 12, h 6 | 0.1-0.3 | present | 16 or 23 × ca. 20.20.0.20.20 (Odhner, 1926) | most probably present | | |
| <i>G. falklandica</i> , holotype, SMNH No. 2304 | Falkland Islands | l 22, b 15, h 11 | 0.1-1 | present, especially laterally | about 17 × 11.15-20.0.15-20.11 (Odhner, 1926) | present | | |

sected. There is no originally designated holotype. A distinct prostate is doubtlessly present in a rather well-preserved specimen (SMNH No. 2306) which is here designated **lectotype** of *Geitodoris patagonica*. The prostate covering the bursa copulatrix was found to be stored in a small vial together with the partly dissected specimen. It is concluded that Odhner misinterpreted the prostate as part of the female glands in both *Geitodoris patagonica* and *G. falklandica*. This might be due to the fact that the genus *Geitodoris* was clearly defined by radular criteria but believed to lack a distinct prostate at the time of Odhner's study (see generic discussion: Odhner, 1926:78–80).

Owing to the presence of numerous subepidermal notum glands, the specimens examined during the present study agree with the original description and with type material of *G. patagonica* (see Figures 5C, D). In contrast, *G. falklandica* was originally described as lacking such glands (Odhner, 1926). The holotype of *G. falklandica* indeed has a comparatively thin, somewhat squeezed notum. In lateral areas, however, there clearly are large saclike glands within the notum (see Figures 5A, B). The quantity of glands present in certain areas of the notum varies intra-individually and between recently collected specimens from the same population and is strongly influenced by preservation (personal observation). Thus there remains no reason to doubt the conspecificity of *G. patagonica* and *G. falklandica*. Both species were established within the same study; priority is given to *G. patagonica* Odhner, 1926, due to its name better reflecting the geographical distribution of the species and to its original description giving more details on the characteristic notum consistency. A single specimen from Puerto Quequén, Argentina was assigned to *G. patagonica* (as "*Geitodoris patagonicus*") by Carcelles (1944) with some reservations. Since no description was given, this record needs to be confirmed.

Geographical distribution: *Geitodoris patagonica* was known previously from Puerto Madryn (about 42°30'S), Argentina (Odhner, 1926) south to Bahía Camarones (44°53'S, 65°39'W) (Schrödl, 1996b). The identification of material collected during the French Cape Horn Expedition in 1882–1883 as *G. patagonica* extends this range south to Orange Bay, Hoste Island, Chile (Figure 9). The synonymy with *G. falklandica* includes the Falkland Islands. In contrast to *Diaulula hispida* and several other Magellanic nudibranchs which occur on both the Atlantic and the Pacific coasts of Patagonia (Schrödl, 1996a, b, 1997a, b, c; this study, Figure 3), *G. patagonica* at the moment appears to be limited to Atlantic waters south to Tierra del Fuego and adjacent islands having a Falkland Current-related distribution (Figure 9). However, this picture may change with a better faunal knowledge of the southern Chilean fjord region and improved taxonomy.

Generic comparison: In recent reviews (Ortea & Ballesteros, 1981; Ortea, 1990; Miller, 1996) the genus *Geitodoris* was mainly characterized by the presence of spatulate (lamellate, platelike) marginal radular teeth, in addition to, but clearly differing from, more or less hook-shaped lateral teeth. The presence or absence of a distinct prostate has been used as an important character to distinguish species within the genus *Geitodoris* as well as to define subgenera.

Four species with smooth lateral teeth and without a differentiated prostate (*G. complanata* (Verrill, 1880); *G. immunda* Bergh, 1894; *G. mollina* Bergh, 1904; and *G. lutea* Baba, 1937) were placed into the subgenus *Geitodoris* Bergh, 1891 (type species: *G. (G.) complanata*) by Ortea & Ballesteros (1981). However, a curved "prostate" was explicitly mentioned in the original description of *G. immunda* by Bergh (1894), and Baba (1937) did not describe the genitalia of *G. lutea* at all. Miller (1996) added *G. reticulata* Eliot, 1906, to the subgenus *Geitodoris sensu stricto*. Curiously, Cervera et al. (1985) previously considered *G. reticulata* to be a junior synonym of *G. planata* (Alder & Hancock, 1846), a species described as having a distinct prostate in the same study. In addition, *Geitodoris patagonica* and (its synonym) *G. falklandica* were assigned to the subgenus *Geitodoris s. s.* by Miller (1996). However, since *G. patagonica* is shown herein to possess a distinct prostate, this species must be re-compared with congeners having a prostate.

Species assigned to the subgenus *Carryodoris* Vayssière, 1919 (type species: *G. (C.) joubini*) by Ortea & Ballesteros (1981), *Geitodoris joubini* (Vayssière, 1919), *G. oshimai* (Baba, 1936), and *G. portmanni* (Schmekel, 1970) have serrate lateral teeth and clearly differ from *G. patagonica*, which has simple hooked laterals. The presence of a prostate in *Carryodoris* assumed by Ortea & Ballesteros (1981), however, was only confirmed for *G. portmanni* (see Schmekel, 1970; Schmekel & Portmann, 1982; Perrone, 1984).

Geitodoris patagonica agrees with species of the subgenus *Verrillia* Ortea & Ballesteros, 1981 (type species: *G. (V.) bonosi*), which according to Ortea & Ballesteros (1981) and Miller (1996), are characterized by a distinct prostate and smooth laterals. In *Geitodoris bacalladoi* Ortea, 1990, and *G. sticta* Miller, 1996, a vestibular gland is absent (Miller, 1996), whereas *G. patagonica* clearly possesses a tubular vaginal gland (Odhner, 1926; this study). *Geitodoris bonosi* Ortea & Ballesteros, 1981, was said to have a penial gland, but figure 3 of the same paper (Ortea & Ballesteros, 1981) shows a gland opening as close to the vagina as to the male duct. In contrast to *G. patagonica*, which has a receptaculum seminis on a short stalk, *G. bonosi* is described as having a serially arranged receptacle (Perrone, 1992). *Geitodoris perfossa* Ortea, 1990, *G. capensis* Bergh, 1907, *G. planata* (Alder & Hancock, 1846), and *G. pusae* (Marcus, 1955) are all distinguishable from *G. patagonica* due to their yellow, orange,



Figure 9

Geographical distribution of *Geitodoris patagonica*.

reddish, or brownish coloration with white and brownish patches on the notum (see Ortea, 1990; Miller, 1996). *Geitodoris patagonica* has a whitish notum with irregular black spots (Schrödl, 1996b). *Geitodoris pusae* is unique in having spicules (Ortea et al., 1988; Ortea, 1990) or cuticular spines (Marcus & Marcus, 1967) within the distal portion of the vestibular gland. *Geitodoris immunda*, never placed in *Verrillia*, although possessing a prostate (Bergh, 1894), has serrate marginal teeth, whereas the marginals are smooth or irregularly worn in *G. patagonica*.

Miller (1996) discussed four additional species as possibly belonging to the genus *Geitodoris*, but marginal radular teeth remain to be confirmed as lamellate in *Discodoris palma* Allan, 1933, *Discodoris crawfordi* Burn, 1969, and *Discodoris millegrana* (Alder & Hancock, 1854). Only one species, *Geitodoris heathi* (MacFarland, 1905) resembles *G. patagonica* due to the possession of lamellate marginal teeth, and of prostate, vestibular, and saclike mantle glands (Marcus, 1961; Millen, personal communication). All the above species differ from *G. patagonica* in having orange or brownish pigmentation.

Discodoris mavis Marcus & Marcus, 1967, a species very similar to *G. heathi*, is transferred to the genus *Geitodoris* herein due to its spatulate marginal teeth. It resembles *G. patagonica* in having a swollen prostate, a vaginal gland, a stalked receptaculum seminis and saclike mantle glands, but differs in its orange coloration (Marcus & Marcus, 1967). *Discodoris tema* Edmunds, 1968, from Ghana is also transferred to the genus *Geitodoris*. This is due to the possession of close-standing, spatulate marginal teeth (see Edmunds, 1968:fig. 7) clearly differing in shape from the simple hamate laterals. This orange species externally differs from *G. patagonica*, but closely resembles *G. perfossa* Ortea, 1990. In conclusion, *G. patagonica* is a valid species and does not appear to have any synonyms beside *G. falklandica*.

Within nudibranchs close-standing, spatulate marginal radular teeth are restricted to members of the genus *Geitodoris*. Presuming this unique character to be derived from uniform, hamate teeth (Gosliner, 1994) only once, the genus *Geitodoris* would be a monophyletic group. In contrast, the subgenera established by Ortea & Ballesteros (1981) were defined on the base of character combinations. Therefore, they do not necessarily reflect natural groups, and future cladistic analysis would be desirable.

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